

II.—On the Development of the Calcispongiæ.

By ELIAS METSCHNIKOFF*.

[Plate II.]

DURING my residence at Messina in the spring of 1868 I made some observations on the development of *Sycon ciliatum* (*Sycandra raphanus*, Häck.), which I have not hitherto published, because I did not consider them sufficiently complete†. But now, since the appearance of Häckel's 'Monograph of the Calcispongiæ'‡, I feel compelled to publish my investigations. The reasons which have moved me to hesitate no longer in doing this will be clear enough from what follows.

I hope that my memoir, small as it is, will not be passed unnoticed by the readers of Häckel's three-volume monograph, inasmuch as it is devoted exclusively to developmental history, *i. e.* to that department of zoology the great importance of which in morphological questions seems to be now generally recognized. With regard to the special case before us, that of the Calcispongiæ, the important part of developmental history is strongly insisted upon by Häckel; but unfortunately the investigations of that naturalist relating to this subject are so defective that a fresh treatment of the matter has become a pressing necessity.

I pass now to the description of my investigations. When we examine transverse sections of sexually mature *Syca*, we observe beneath the entodermal lining a great number of ova and embryos in very different stages of development. The total and regular segmentation takes place in the same way as is described by Häckel in *Sycyssa Huxleyi* and *Leuculmis echinus*. We have only to remark that a small so-called segmentation-cavity (Pl. II. fig. 2, *c*) is formed, which, however, soon disappears (fig. 3). As the result of the process of segmentation a roundish embryo (fig. 4) is produced, on which a great number of small cells are to be detected. I could not succeed in discovering any process of differentiation in the embryo, for which reason the question of the origin of the germ-lamellæ must remain undecided. Evidently the stages are too quickly passed through for them to be accurately observed. I must therefore pass on at once to the description

* Translated by W. S. Dallas, F.L.S., from the 'Zeitschrift für wissenschaftliche Zoologie,' Band xxiv. (1874), pp. 1-14, pl. i.

† I have already given a short account of them in my annual report upon the progress of developmental history, printed in Russian.

‡ 'Die Kalkschwämme: eine Monographie.' 3 vols. Berlin, 1872. In this paper I shall only quote the first volume of this work.

of the formed larva, which has already been observed in the same species by Lieberkühn, and in the nearly allied *Dunsterwillia coreyrensis* (*Sycandra Humboldtii*, Häck.) by Oscar Schmidt. In agreement with these naturalists, especially the latter, I have found all normally developed swarming *Sycon*-larvæ divided into parts of nearly equal size, only one of which appeared to be composed of vibratile cylindrical cells, and the other of unciliated spherical cells (fig. 5). The former portion constituted a sort of hemisphere containing in its interior a central cavity of no great size, in the vicinity of which a great number of very fine brown pigment-granules were accumulated (fig. 5, *g*).

If two or three specimens of sexually mature *Syca* are kept only for a few days in small glass capsules, the larvæ swarm out in great quantities in order to become further developed, *i. e.* to attach themselves. To observe the subsequent processes, all that is necessary is to put a few object-bearers at the bottom of the glass capsules, so that they may serve as points of adhesion for the larvæ; but even without this precaution the adherent young sponges may be detected, as they adhere to all objects existing in the vessels, even the smallest.

The first process of postembryonic development consists in the complete disappearance of the central cavity, by which the upper (*i. e.* the vibratile) half of the larval body is perceptibly reduced in size (fig. 6)*. Then commences the fusion of the spherical cells of the hinder part into a compact mass—only one row, of the spherical cells in immediate contact with the vibratile epithelium, being an exception, as these still retain their integrity for a considerable time (figs. 6, 8, 9, *d*). The larvæ often attach themselves even during this stage; but not unfrequently they continue for some time longer in their swarming activity, but without being thereby hindered in their development. As one of the most important processes occurring in this, the formation of the calcareous spicula must be specially noticed. The rather brownish, unciliated, compact mass of the hinder portion is the place in which the skeletal structures originate; to be convinced of this, one need only glance at figs. 7 and 8. It must also be mentioned as worthy of notice that at first only long rod-like spicula are formed; so that at this early stage our *Sycon* passes through a state which is persistent in the genus *Sygyssa*, a fact which may be of significance in phylogenetic considerations.

The principal thing in the metamorphosis is that the un-

* The above-mentioned brown mass of granules collected into a central aggregation, as shown in figs. 6-8.

ciliated (posterior) half becomes converted into the skeleton-forming layer; whilst the anterior* ciliated section draws back into the interior of the larval body, to form the entoderm. That the half of the body consisting of what Hæckel calls flagellated cells actually draws back into the interior is convincingly shown by comparing with each other the four larval stages represented in figs. 5 to 8. It will be seen that in each stage it projects less and less, while the skeleton-forming layer, on the contrary, becomes proportionately larger. In order to obtain a notion of the mode in which the ciliated half retracts itself, we must examine larvæ which have adhered rather early, *i. e.* before the formation of the skeleton. In these we can see that, while the hinder half has altered very little, the anterior ciliated section becomes invaginated in the interior of the body (fig. 9), by which means, of course, an aperture (aperture of invagination, fig. 9, *o*) is produced at the upper pole. The ciliated hemisphere consequently forms a sac-like body, which appears to be surrounded by the skeleton-forming layer. It appears from the next following stages that the aperture of invagination just mentioned does not pass directly into the definitive osculum, but becomes entirely effaced. Hence, in its further development, the young adherent sponge appears as a perfectly closed body, in which two principal constituents may be clearly distinguished (fig. 10). Externally there is the skeleton-forming layer, in which several rod-like spicules are enclosed; in the interior, on the contrary, there is a closed body, which represents the entoderm. The walls of the latter appear so thick that for a time one is unable to detect any cavity; this comes later into view, when the double-layered wall becomes formed into a vesicle. In the sponge three days old, represented in fig. 11, I could already observe an internal cavity (fig. 12, *c*), but it was still very narrow and small. It was only in a larger *Sycon*, six days old, that a considerable cavity was to be seen; it shimmered through the body-walls even in the living animal (fig. 13). When this same animal was treated with acetic acid, the two vesicularly inflated layers † (fig. 14, *a, b*), as well as the internal gastro-vascular cavity (fig. 14, *c*), could be most clearly distinguished. In this stage, the latest that I have seen, no buccal aperture was yet formed; on the other hand, three-pointed spicules were already present.

* As regards the designations "before" and "behind" I agree, upon developmental historical grounds, with Lieberkühn and Schmidt, but not with Hæckel.

† It is to be remarked that I could detect no cilia on the entodermal cells of this stage.

From the preceding it follows that the two principal layers of the sponge-body are founded already in the body of the larva, and, further, that the upper ciliated half of the body is converted into the entoderm, and the lower unciliated half into the layer surrounding the entoderm.

Having now communicated the facts of my investigations, the question may be put, How far can the results obtained by me be brought into accordance with Hæckel's statements? At pp. 34 and 216 of his work this naturalist gives the following short summary of the developmental phenomena in the Calcispongiæ:—"From the egg is produced, in consequence of total regular segmentation, a simple spherical or elongated round body, which is at first composed of homogeneous spherical cells. Then there is produced in the interior of the cell-aggregate a small central cavity (the stomach), which, breaking through outwards, forms an orifice (the *osculum* or buccal orifice). The surface becomes covered with cilia; and then the embryo swims about as a free larva (*planula*) for a long time. The body-wall (of the larvæ) consists of two layers of cells, entoderm and exoderm. The inner layer, or entoderm, consists of a layer of unciliated cells; the outer layer or exoderm consists of a layer of ciliated cells (flagellate cells)." Then "the larva falls to the bottom, and attaches itself. The attachment takes place at the pole of the longitudinal axis, opposite to the buccal orifice (aboral pole), by a flat or peduncular surface of adhesion, which from this time forth forms the base of the sponge-body. The flagellate cells of the exoderm now retract their flagellar filaments, coalesce to form the syncytium, and begin to secrete their interior protoplasmic products, the calcareous spicules. The cells of the entoderm, on the contrary, which were previously not ciliated, stretch forth each a long vibratile process, and thenceforward line the surface of the stomach as a flagellate epithelium."

This description therefore runs quite differently from that given by me above; for according to Hæckel the skeleton-forming layer (exoderm, Hæck.) originates not from the unciliated cells, but from so-called flagellate cells provided with long cilia; and the converse is the case with the entoderm, which Hæckel derives from spherical cells, whilst, according to my observations, it takes its origin from the ciliated (or flagellate) cells. This is the chief difference in our statements, the elucidation of which will here be attempted. Hæckel describes the larvæ of four species of Calcispongiæ, of which those of *Syeyssa Huxleyi* exhibit the greatest analogy with the larvæ of *Sycon*, inasmuch as they appear to be com-

posed of two dissimilar halves (only one of which is clothed with cilia). But as, according to Hæckel, the course of development agrees in essentials in different Calcispongiæ, we must deal with his representation as general.

With regard to the first stages (embryonic development), my observations are in accordance with those of Hæckel; but this only renders the difference as to the later states more remarkable. Besides that according to Hæckel the internal cavity in the larvæ is always lined with a particular layer of spherical cells, whilst Oscar Schmidt and myself detected nothing of the kind, Hæckel's description deviates most widely from mine with respect to the postembryonic development. He makes no mention either of the invagination of the ciliated layer or of the hypertrophy of the unciliated layer; the whole metamorphosis is supposed to be reduced to this—that the ciliated exoderm retracts its flagellar filaments and becomes converted into the so-called "syncytium," while the entoderm of the larva acquires cilia in order to furnish the so-called flagellate epithelium. The reason why these views are so directly opposed to mine is easy to find, if we carefully peruse the chapter on the developmental history of the Calcispongiæ (pp. 328–338). From this it appears that Hæckel never observed the postembryonic development in the sponges, but has invented it *à priori*. The following passage is very instructive:—"The conversion of the swimming *Gastrula* into the youngest and simplest attached state, which we will call *Ascula*, appears to take place very rapidly and *has not yet been observed. The changes occurring therein may, however, be directly inferred from the comparison of the Ascula and Gastrula (!)*. The attachment of the latter takes place at the aboral pole of the longitudinal axis, at the end opposite to the buccal orifice. The flagellate cells of the dermal lamella suspend their vibratile movements, retract the flagellar process, and lose their slender cylindrical form, flattening and spreading out into the extending intestinal surface. The unciliated entodermal cells, on the other hand, divide repeatedly and then become converted into flagellate cells, each of them extending a filiform flagellum from its proximal end, or that turned towards the stomachal cavity" (p. 337). But even this is not all! Hæckel says that he has "inferred" (*erschlossen*) the metamorphosis of the Calcispongiæ from the comparison of the *Gastrula* with the *Ascula* (*i. e.* "the youngest and simplest attached stage"); but nowhere does he give either a description or a figure of even a single actually observed *Ascula*! From this we may infer that he has really never seen an *Ascula*; for otherwise he

would have said something about it, especially seeing that in general he describes his subjects diffusely and circumstantially (as, indeed, may be seen from the quotations just given). It is evident that he has compared the free-swimming larva with a young but on the whole fully-formed sponge, without considering that in this way he might very easily be led astray, as in fact has happened. The most remarkable circumstance is that, in several parts of his monograph, Hæckel puts forward his "directly inferred transformation" as an actually existing fact, and not as a more or less probable hypothesis. Thus, for example, he says at p. 160, "I give the name of syncytium in the Calcispongiæ to the whole mass of tissue which *is produced by the fusion of the cells of the exoderm of the ciliated larva*;" and at p. 216, "Each cell of the entoderm *stretches forth a long vibratile process &c.*" In these cases he forgets entirely that he has never seen either the fusion or the extension of the cilia*. Is this the philosophical "method of scientific investigation" so celebrated by Hæckel, and for the non-employment of which the embryologists (ontogenists) are so severely blamed by him?† (p. 472).

I now pass to the question how far the developmental history of the Calcispongiæ can be made available for the comparison of the principal layers of these organisms with those of other animals. In this respect Hæckel has arrived at a settled conclusion. He regards as one of the most important results of his work the statement that the two layers of the sponge-body are homologous with the ectoderm and entoderm of the Cœlenterata. By the ectoderm (or exoderm) he understands the so-called syncytium—that is, the skeleton-forming outer layer of the sponge, whilst he characterizes the flagellate epithelium as the entoderm. He gives this conclusion as the result of his investigations in developmental history. Thus he says, for example:—"The relationship of

* I must indicate the following passage as exceedingly naïf:—"The structure of the flagellate cells of the exoderm in the *Gastrula* is exactly similar to that of the flagellate cells of the entoderm in the fully developed Calcispongia" (p. 335). And yet this striking agreement did not suffice to raise any doubt in Hæckel as to whether his *à priori* conception of the germ-lamella represents the truth.

† It is truly surprising to read how this method has been employed in the representation of the *Ascula*, *Protascus*, *Protospongia*, and other form-stages invented by Hæckel. Thus, for instance, it is said at p. 339:—"Formerly I *supposed* that all Calcispongiæ in their earliest youth pass through the characteristic form of the *Protolynthus*. But I must now add as a limitation that *in many cases* the transition from the *Ascula* to the *Olynthus* takes place not through the *Protolynthus* but through the *Protospongia*." All these conclusions are assumed without any single fact ascertained by observation being cited in their support.

the Sponges to the Coelenterata, and the comparison of the 'water-vascular system' of the former with the 'gastro-vascular apparatus' of the latter, which Leuckart first indicated, has then been demonstrated (?) more circumstantially and firmly established by developmental history in my memoir 'Ueber den Organismus der Schwämme' &c. I therein proved that a true homology really exists between these two systems of canals, and that the wall of these canals in the Sponges, as well as in the Hydromedusæ, Ctenophora, and Corals, is formed from two originally different cell-layers or lamellæ—namely from the exoderm, which represents the outer, and the entoderm, which represents the inner germ-lamella of the higher animals. I further demonstrated that these two primitive formative membranes show the same characters in the ciliated larva developed from the egg in both the groups of the Coelenterata and Sponges" (p. 214; see also p. 33). As we have seen that one of the principal momenta in the developmental history of the Calcispongiæ, the metamorphosis, was not observed but constructed *à priori* by Hæckel, and further that this construction is contradicted by facts, of course the just cited opinion as to the germ-lamellæ of the sponges must also be subjected to a thorough revision.

I will first consider Hæckel's statements, and then pass to the expression of my own views. Hæckel has expounded his theory most completely in the last section of his first volume ("Philosophie der Kalkschwämme"). We find there the following passages:—"If we compare the coarser and finer structural characters of *Hydra* and *Cordylophora* . . . with the corresponding structural characters of *Olynthus**, we cannot but be astonished at the striking agreement which occurs even in minute details" (p. 460). Now in what does this astonishing agreement consist? "1, the simple stomachal cavity with buccal orifice; 2, the composition of their stomachal wall of two lamellæ, the ciliated entoderm and the unciliated exoderm; 3, the composition of the entoderm of flagellate cells" (p. 460). The differences cited by Hæckel are as follows:—"1, the constitution of the exoderm, the cells of which in *Hydra* and *Cordylophora* develop urticating capsules and neuro-muscular processes, but in *Olynthus* fuse into the syncytium; 2, the circlet of tentacles of the former, which is wanting in the latter; 3, the different origin of the sexual organs." "It will be seen at once that in the first three points an homology of the entoderm alone can be spoken of, since for

* By *Olynthus* Hæckel understands a simple, solitary calcareous sponge with double walls (ectoderm and endoderm), and with a spacious sacci-form "stomachal cavity."

the agreement of the outer layer only the absence of cilia, a negative and unimportant character, has been cited. But as regards the differences, the different structure of the outer layer must be placed in the first rank. Hæckel endeavours to get over this difficulty, saying:—"but this [difference in the structure of the exoderm] is to be regarded as a secondary histological differentiation of the two divergent groups" (p. 460). Although he cites no evidence of this, he has no hesitation in explaining the "differences in anatomical structure between the simplest hydroids and the simplest sponges" as "*of quite subordinate significance*" (p. 460). But is it really so insignificant that the outer layer of the sponge exclusively produces all skeletal formations, whilst in the true Cœlenterata these are never developed from the ectoderm, but always from the cutis (therefore from the mesoderm)? Where do we know of any examples of an epithelial tissue (to which the ectoderm of the Cœlenterata belongs) serving as the seat of the formation of a calcareous skeleton? These are questions for an answer to which we may seek in vain from Hæckel.

Let us return to Hæckel's argumentation:—At p. 461 we read as follows:—"Of the greatest significance is the ontogeny of *Cordylophora*, which *perfectly agrees with that of Olynthus*." Unfortunately Hæckel knows so little of the ontogeny of *Olynthus*, that he has no right to say any thing about this "perfect agreement." As we have seen, Hæckel has invented the metamorphosis of the Calcispongiæ (without hitting upon the right thing), in doing which he evidently took the agreement with the Hydroida as his starting-point, instead of arriving at it as a result. In my opinion the metamorphosis "directly inferred" by Hæckel is nothing more than a cast (*Abklatsch*) from the well-known metamorphic history of the Hydroida. Hæckel says with particular emphasis that "the *Planula* and the *Planogastrula* are perfectly alike in both animals;" but that proves nothing so long as neither the origin nor the metamorphosis of the ciliated larva has been observed*.

Hæckel may repeat, as often as he pleases, that he was the first to *demonstrate* the homology of the two lamellæ of the Sponges and Cœlenterata †; but every critically thinking naturalist will at once see that this is not the case, and that in

* The transformation of his "*morula*" into the swimming larva has not been observed by Hæckel any more than by myself; he has neither described nor figured any transition-stage; nevertheless he feels justified in filling up the existing gap *à priori*, without, however, expressly saying so.

† See the above-cited quotations from p. 214, and, further, pp. 33, 456, and 470.

reality Hæckel has furnished no proof at all of the homology of the ectoderm and the skeleton-forming layer. But it would also not be difficult, by the aid of facts already sufficiently well known, to convince ourselves that no such homology exists in nature. We need only take into consideration the known points in the developmental history of the marine siliceous sponges*. It is known that in the embryo of these animals the whole cell-mass divides into two portions, of which the outer becomes the ciliated epithelium, whilst the *inner* takes on the character of a *skeleton-forming* cell-aggregate. The topographical position of this inner cell-mass (beneath the ciliated layer), the circumstance that it appears as an aggregate of compact spiculigenous elements, and, further, the fact that these cells never appear as ciliated epithelial cells, furnish us with sufficient data for rejecting their supposed homology with the ectoderm of the Cœlenterata. To this of course must also be added the argument above cited, that the ectoderm of the Cœlenterata never produces skeletal structures, which always appear as derivatives of the cutical layer. I have designedly left out of consideration the facts observed by me in the developmental history of the *Sycon*, in order to show that by careful consideration of the known material it is impossible to arrive at the erroneous notion of the agreement of the skeleton-forming layer with the entoderm. But if we will also consider the facts above described, we shall see at once that the development of the Calcispongiæ is likewise opposed to Hæckel's interpretation. It was established that it is the hinder unciliated half that furnishes the calcareous skeleton, and consequently that the skeleton-forming elements never appear in the form of flagellate or ciliated epithelial cells, which are characteristic of the ectoderm of the Cœlenterata.

From the reasons adduced, I venture to draw the conclusion that the skeleton-forming layer of the sponges, or the so-called "syncytium," of Hæckel, does not represent the ectoderm, but the skeleton-forming layer of many other animals, especially

* See, *e. g.*, the investigations of Lieberkühn. I have myself made some observations upon the development of the siliceous sponges, which I shall publish elsewhere. Here I limit myself to the remark that the larvæ of four genera (*Reniera*, *Esperia*, *Raspailia*, and an undetermined genus) are essentially of similar structure. As an example I have figured the larva of *Reniera* (Plate II. fig. 15), which is chiefly distinguished from the others by the presence of a posterior cirlet of cilia. I have observed the metamorphosis in an *Esperia*. The external epithelial layer is gradually lost, so that for a time the young sponge appears to be composed of an irregular aggregation of parenchyma-cells. It is only subsequently that the so-called ciliary baskets (*Wimperkörbe*) appear, in the form of closed spheres, which as yet are in no way connected with each other.

Cœlenterata and Echinodermata, and consequently belongs to the domain of the middle lamella (*mesoderm*, Hæckel). Besides the points cited, the fact that the cells of the middle lamella in both the Cœlenterata and the Echinodermata (at least in the young state) are exceedingly changeable, may also be adduced in favour of this view. Thus, for example, we see that the naked amœboid cells of the skeleton-forming layer in the larvæ of Echinoderms move about in the body-cavity, and, in consequence of active movements, collect in particular spots, *e. g.* in the stone-canal.

In order to explain my view still more clearly, I will here compare with each other three objects which are at the first glance very similar. If we examine the three figures here given (A, B, C), we observe that all three consist of a one-layered

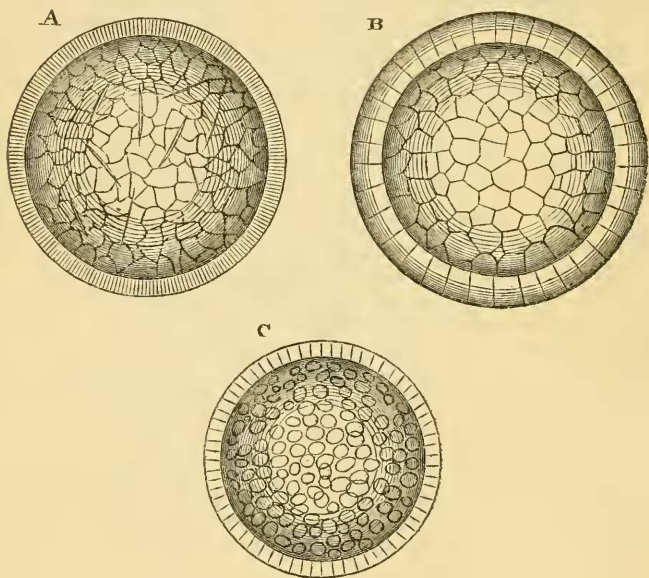


Fig. A represents an embryo of *Reniera*, B an embryo of *Sertularia*, and C an embryo of *Echinus*.

sphere, densely packed with a compact cell-mass. If it were possible in the comparison to take only such data into consideration, we should say (as Hæckel actually has done with regard to the planulæ of the Sponges and Hydroïda) that all the three embryos are perfectly homologous, and especially that all three have originated in a similar manner. It is only the close examination of subsequent stages that shows us that the homo-

logy can be accepted only for two embryos. The one-layered external envelope is in all three cases the dermal layer, which afterwards becomes covered with cilia and represents an epithelial tissue, which may be characterized throughout as the ectoderm. In the siliceous sponges this layer is only of short persistence; it disappears during the transformation into the attached form. In the *Echini* also the ectoderm is only provisional, at least upon many parts of the body. In the Hydroida, on the contrary, it persists throughout life, as is sufficiently well known. The inner cell-mass, in our three cases, experiences the following alterations: in the siliceous sponges it furnishes (at least for the most part) the skeleton-forming layer, becoming converted into the so-called synectium of Hæckel; in the *Echini* it plays a perfectly similar part, although the cellular elements here retain their individuality; but it is quite otherwise in *Sertularia* (and the Hydroida in general), in which the cell-mass, although similar in appearance, becomes the entoderm.

The conclusion at which I have arrived is, that the synectium corresponds to the skeleton-forming layer of the Echinodermata (and Cœlenterata), whilst the ectoderm (in the siliceous sponges) appears as a provisional structure confined to the larval stage. (With regard to the inner layer (*b*) of our three embryos, a still more profound analysis may be instituted; we may elucidate the question as to the homology of this layer by the consideration of the mode of origin of the mesoderm. But this we shall pass over, so as not to depart from the principal theme, especially as at the moment several important facts are still insufficiently known.)

What, then, is the position of the Calcispongiae in relation to the question of the germ-lamellæ? With regard to this order in general nothing definite can be said at present, as the larvæ of different representatives of the order appear to be constructed in various ways, while the history of the metamorphosis is known only in the case of a single species. But if we take this species alone into consideration, we may, by comparison with the better-known siliceous sponges, obtain an understanding of many circumstances. Above all it must be borne in mind that the larvæ of four genera of marine siliceous sponges observed by me always have a gap in the ectoderm at the posterior end of the body through which the skeleton-forming layer projects outwards. Now this baring, which, indeed, is very peculiar, occurs in a still greater degree in the *Sycon*-larvæ, which is in connexion with the weak development of the ciliated layer. The latter, instead of forming a sphere as in so many other animals, remains only in the form of the

segment of a sphere, which is afterwards invaginated to constitute the entoderm. Of the four larvæ described and figured by Hæckel, that of *Sycyssa Huxleyi* is most nearly allied to the *Sycon*-larvæ, although the former is strikingly distinguished by the presence of a layer of spherical cells lining the internal cavity. How the metamorphosis takes place in this and in the other three cases (*Ascetta mirabilis*, *Asculmis armata*, and *Leuculmis echinus*) I cannot say in the present state of our knowledge.

After what has been said, I need hardly say particularly that all the inferences founded by Hæckel upon the "homology" of the sponge-larvæ (*Gastrula*) with the larvæ of other animals, collapse of themselves, because they are destitute of all solid grounds.

In conclusion, I will make one or two remarks upon the question of Cœlenterism, but without entering into any detailed discussion, as I have elsewhere (in the concluding chapter of my "Studien über die Entwicklung der Medusen und Siphonophoren," appearing simultaneously with this paper*) treated this question in detail. Here I will only endeavour to show that the opinions expressed by Hæckel are by no means capable of shaking my theory† as to homologies of the cœlenteric apparatus, inasmuch as they for the most part rest upon misconceptions. Hæckel's course of thought is as follows:—1, "the true body-cavity," which occurs only in the Vermes‡, Echinodermata, Arthropoda, Mollusca, and Vertebrata, "always originates by a cleaving of the mesoderm;" 2, "as the mesoderm is entirely wanting in the sponges, there can be no body-cavity in them—nor does it occur in the Cœlenterata;" 3, "the true body-cavity can never, like the intestinal or stomachal cavity, be surrounded by the entoderm;" 4, "consequently also the cavities of the gastro-canal-system in the Sponges and Acalephs are not body-cavities, but an intestinal cavity" (p. 469). To this I must object:—1, the body-cavity in many animals

* Zeitsch. für wiss. Zool. Band xxiv. (1874) pp. 15-83.

† This theory is that the gastrovascular apparatus of the Cœlenterata corresponds to the complex of organs which in the Echinodermata is formed from the lateral diverticula of the primitive intestine. Consequently the peritoneal cavity with the water-vascular system is to be regarded as the homologue of the gastrovascular system. This theory is supported by a whole series of facts, as is more particularly explained in my memoir just cited.

‡ It may here be mentioned in passing that the notions accepted by Hæckel of the *Vermes acelomi* and *V. celomati* by no means possess the importance which that naturalist ascribes to them. The Nemertina and Microstomea have a "true body-cavity" as well as several Trematoda, at least in the states of rediæ and sporocysts.

does not originate by cleaving of the mesoderm, and may even exist without it; thus, a body-cavity exists in several larvæ of Cœlenterata in the space between the ectoderm and entoderm; 2, the Sponges possess the mesoderm in the form of the skeleton-forming layer (see above); 3, the inner cavity of the Echinodermata (which Hæckel regards as a true "body-cavity") is enclosed by the entoderm, as it is produced as a derivative of the primitive intestine. Thus we see that Hæckel's three fundamental opinions will not hold good; and for this reason the fourth point remains without a foundation.

The whole question of Cœlenterism turns upon the idea of the body-cavity. As soon as we without further consideration conceive the inner cavity of the Vermes, Echinodermata, &c. as a "true body-cavity," we place ourselves upon false ground; for that which in different animals acts as a body-cavity, represents structures which are morphologically quite different. Thus we see that in the Echinoderm-larvæ a spacious body-cavity is formed which stands in no genetic connexion with the definitive cavity of the body; the latter originates in the interior of the so-called lateral disks, which, in the last resort, take their origin from the primitive intestine. The Cœlenteric apparatus is to be paralleled with the peritoneal cavity of the definitive Echinoderm-body, not with the body-cavity of the Echinoderm-larva.

EXPLANATION OF PLATE II.

- Fig. 1.* Portion of a transverse section through the *Sycon*-tube with two segmented germs.
- Fig. 2.* A segmented germ with segmentation-cavity (*c*).
- Fig. 3.* A somewhat later stage.
- Fig. 4.* Portion of a transverse section with an embryo.
- Fig. 5.* The free-swimming larva: *g*, aggregation of granules.
- Fig. 6.* A later larval stage: *d*, individual cells; *g*, aggregation of granules.
- Fig. 7.* A free-swimming larva with skeleton-formation already commenced.
- Fig. 8.* A somewhat further developed larva: *d*, individual cells.
- Fig. 9.* An attached larva without calcareous skeleton: *o*, orifice of invagination (half diagrammatic); *d*, individual cells.
- Fig. 10.* An attached larva with calcareous spicules: *a*, outer; *b*, inner layer.
- Fig. 11.* A young *Sycon*, three days old.
- Fig. 12.* A similar stage, treated with acetic acid: *a*, *b*, as in fig. 10; *c*, gastrovascular cavity.
- Fig. 13.* A young sponge, six days old.
- Fig. 14.* The same treated with acetic acid: *a*, *b*, *c*, as in figs. 10 & 12.
- Fig. 15.* A free-swimming larva of *Reniera* from the Crinæa: *e*, outer ciliary layer; *m*, inner skeleton-forming cell-mass.